A TAXONOMIC STUDY OF LILIACEAE SENSU LATO:
II. EVALUATION OF ENGLER'S SUBFAMILIES

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Introduction

In our previous paper (Badawi & Elwan, 1986) a taxonomic arrangement of 255 species representing 104 genera of the Liliaceae sensu Engler (1888) has been proposed. Several taxonomic treatments of the Liliaceae are already on record (Lindely, 1853; Bentham & Hooker, 1862-1883; Krause, 1930; Lawrence, 1951; Melchoir, 1964; Dahlgren, 1976; Cronquist, 1968; Thorne, 1968; Hutchinson, 1973; and Takhtajan, 1980). Hardly any two of these classifications are in full or near full agreement, and the discrepancies between them go as far as splitting the family into several splinter families. Furthermore, what might be regarded as a tribe by one author is raised to family by another or reduced into a subtribe by a third. Therefore, it is imparative to test our preposed arrangement against other systems. That of Engler (1888), being the most comprehensive and dtailed account of the family has been chosen for this purpose.

In comparing classifactory systems, hierarchical levels of the groups (or taxa) to be compared have to be pre-determined. In this study we have endeavoured to select levels which would lead to maximum resemblance between these taxa in our scheme and those in Engler's system.

COMPARISON WITH THE ENGLEREAN SYSTEM

The tabulated sort of comparison between our arrangement (Badawi & Elwan, 1986) and that of Engler (1888) seems most profitable. Two tables have been, therefore, constructed. Table 1 is made at the 4 GROUPs level of our arrangement, while Table 2 is made at the 9 Groups level .

It is evident from Table 1 that 5 out of the 11 subfamilies of Engler's Liliaceae are disrupted at the 4 GROUPs level. Melanthioideae is the most disrupted; it is shared by the four GROUPs and the distribution of its species among these GROUPs shows no concentration in any one GROUP. These disrupted 5 subfamilies are the largest of the family Liliaceae. The other 6 subfamilies are with relatively limited concepts; and these were, therefore, represented by relatively few species in the sample examined to propose our arrangement.

I. Subfamily Melanthioideae:

At the 4 GROUPs level, Veratreae, Anguillarieae, Colchiceae and Uvularieae are homogenous, i.e. appearing in only one of the GROUPs. The former is the only constituent of GROUP I, the latter is in GROUP IV, while the other two tribes are in GROUP II. From these tribes only

Uvularieae become disrupted at the 9 Groups level. Tofieldieae and Helonieae are disrupted at the 4 GROUPs level (Table 2). However, one should point out that the general arrangement of the examined Melanthioideae may be considered as a support to Buxbaum's (1937) Wurmbaeoideae. This subfamily is made to include the tuberous Melanthioideae of Engler viz Anguillarieae, Colchiceae and Uvularieae p.p. (Gloriosa, Littonia and Sandersonia). The first two tribes are in GROUP II; but Gloriosa is in GROUP IV with the examined species of Tricyrtis, Uvularia (Engler's Uvularieae). In other words all the examined Wurmbaeoideae except Gloriosa are in GROUP II (see Badawi & Elwan, 1986). Hegnauer (1963) and Wildman & Pursey (1968) gave chemical supports for the recognition of Wurmbaeoideae. Huber (1969) relied on seed anatomy, had also supported the relationship among the tribes of this subfamily.

Buxbaum's (1937) Colchiceae includes Androcymbium and Colchicum. In our arrangement the former genus is grouped with Anguillarieae in Group II-D; while Colchicum is in Group II-B. In other words, our arrangement coincide with Engler's concept of Colchiceae not to include Androcymbium. Also, Merendera in our arrangement is more related to Colchicum rather than to Dipidax, Androcymbium and Baeometra. Baker (1880) included the last three genera with Merendera (tribe Merendereae). Colchicum is sometimes defined to include Merendera; together with Bulbocodium (Stefanoff, 1926).

The examined 12 species of Engler's Uvularieae (i.e. including Tricyrtis, which is Tricyrtideae by Hutchinson, 1973) are in GROUP IV. Therefore, our arrangement did not emphasize the distinction of Tricyrtis from other Uvularieae. However, Sen (1975) stated that the chromosome number as well as the Karyotype of Tricyrtis indicate that its taxonomic assignement into an advanced tribe Tricyrtideae is justified. Also Cheadle & Kosakai (1971), depending on the type of vessels in stems and roots, emphasized the difference between Tricyrtideae (including Tricyrtis and Sandersonia) and Uvularieae.

The taxonomic affinity of Walleria had received a wide controversy, thus Bentham (1880), Engler (1888), Baker (1897) included this genus in Uvularieae. Hutchinson (1959 & 1973) considered Walleria in Uvularieae, in Dianelleae as well as in Techophilaeaceae. Chaedle & Kosakai (1971) suggested, on anatomical bases, that Walleria should be excluded from Dianelleae, while it could be placed in Uvularieae or Techophilaeaceae. Huber (1969) considered this genus a member of the tuberous Asparagoideae. It was not expected in our morphological and anatomical study of Liliaceae sensu latc to solve such taxonomic conflict of Walleria. However, the results of our investigation emphasized the distinction of Walleria from Uvularieae. At the 9 Groups level of our arrangement the two examined species of Walleria are separated from the other 10 species of Uvularieae (Appendix I in Badawi & Elwan, 1986).

Table 1. A comparison between Engler's subfamilies of Liliaceae and GROUPs I-IV of our proposed arrangement (Badawi & Elwan, 1986) in terms of the number of species representing each subfamily in each of the 4 GROUPs; number between parentheses equal total number of species within groups; '*' indicates the disrupted subfamilies.

Engler's subfamilies	GROUPs of the proposed scheme			
	I(8)	II(69)	III (117)	IV (61)
I. Melanthioideae*	8	16	2	12
II. Herrerioideae	-	-	-	3
III. Asphodeloideae*	-	4	42	2
IV. Allioideae*	-	30	8	-
V. Lilioideae*	-	19	40	-
VI. Dracaenoideae	-	-	12	-
VII. Asparagoideae*	-	-	3	32
VIII. Ophiopogonoideae	-	-	6	-
IX. Aletrioideae	-	-	4	-
X. Luzuriagoideae	-	-	-	4
XI. Smilacoideae	-	-	-	8

II. Subfamily Asphodeloideae:

This subfamily is disrupted at the 4 GROUPs level of our arrangement. However, 42 out of the examined 48 species are in GROUP III (see Table 1). Only two Asphodeloid species are in GROUP II; these are of Lomandreae and Dasypogoneae. These tribes are commonly regarded to be Xanthorrhoeceae rather than Liliaceae (Hutchinson, 1973; and Dalhgren, 1976). No doubt that this grouping of 42 species of Engler's Asphodeloideae in GROUP III out of the examined 48 species avouch the relative homogenity of this subfamily. Nevertheless, at the 9 Groups level, our arrangement raise a taxonomic point of interest considering the status of Aloineae. Members of this group did spilt off from other Asphodeloideae (Table 2). Engler's subtribes of Aloineae, viz Aloineae-Aloinea and Aloineae-Kniphofinae have been raised to tribal rank by many taxonomists (Hutchinson, 1973 and Takhtajan 1980). While Nakai (1942) gave the tribe Aloineae (in its strict sense) the family status "Aloeaceae". And in fact the divergence of Aloineae-Aloinea, in our arrangement from the other examined members of Asphodeloideae, is at a high level of dissimilarity (Badawi & Elwan, 1986). Therefore, our arrangement evokes the acceptance of the family Aloeaceae. Sen (1975) had also pointed out that members of this group have a characteristic karyotype. All having X=7; with 4 very long and 3 very short chromosomes.

III. Subfamily Allioideae:

Many genera of this subfamily are considered in more recent taxonomic treatments (e.g. Traub, 1963; and Hutchinson, 1973) not liliaceous taxa. In our arrangement only 8 species of Alloideae are in GROUP III. These represent the examined species of Agapanthes, Brodieae, Bloomeria, Milla and Miulla (see Badawi & Elwan, 1986). These genera are

Amaryllidaceae in Hutchinson's (1973) system. The relationship of these genera to Amaryllidaceae was ascertained and proved to be based on a number of morphological and anatomical criteria (Badawi & Elwan, 1976).

However, the main bulk of the examined Allioideae (30 out of 38 species) are in GROUP II. These are Tulbaghia (1 species), Allium (15 species), Nothoscordum (3 species), Gagea (8 species), Gilliesia (2 species) and Miesera (1 species). These genera, with the exception of Gagea are in many treatments outside the framwork of Liliaceae, but rather in a much definable family Alliaceae (Dahlgren, 1967; and Takhtajan, 1980). In Hutchinson's (1973) system these genera are Amaryllidaceae, while Gagea is Tulipeae. In our arrangement, GROUP II includes also the examined 17 species of Tulipeae (Table 2). This means that members of Allioideae in GOUPR II share a relatively high similarity to Tulipeae rather than to the 8 species of Alloideae in GROUP III. The taxonomic attitude to consider Gagea as Tulipeae was ascertained on embryological and cytological bases (Kaul et al., 1969; and Sen, 1975). Also on morphological and anatomical bases (Badawi & Elwan, 1976) suggested that Gagea together with Tulbaghia and Gilliesia are better associated with Tulipeae.

IV. Subfamily Lilioideae:

The disruption of this subfamily hits across its two tribes; Tulipeae (17/17 species) is in GROUP II, while Scilleae (40/42 species) is in GROUP III. Thus our arrangement reflects a pronounced distinction between Engler's Tulipeae and Scilleae making the concept of this subfamily rather implausible. The recognition of Tulipeae (including Gagea) and Scilleae as two separate but highly related groups is not debated any more. However, Sen (1975) suggested the exclusion of Colchortus, Llyodia and Gagea from Hutchinson's Tulipeae. He also visualized the fact that Scilleae contains several assemblages but their relationship is not very remote.

V. Subfamily Asparagoideae:

The disruption of this subfamily at the 4 GROUPs level of our arrangement does not reflect serious taxonomic conflict. Since 32 out of the examined 35 species of Asparagoideae are in GROUP IV, while only 2 species of Clintonia (Polygonateae) and one species of Rhodea (Convollarieae) are in GROUP III (Badawi & Elwan, 1986). However, at the 9 Groups level only Pariideae and Asparageae appear intact, while Polygonateae is seriously disrupted (Table 2). The latter tribe was divided by Sen (1975) on cytological bases into 3 tribes. Clintonia and Streptopus in one tribe,while Polygonatum, Maianthemum and Smilacina in other tribe and Disporum in the most primitive tribe. Our arrangement (Badawi & Elwan, 1986) shows that Clintonia is in GROUP III, while the other 11 examined species of Polygonateae (Streptopus, Polygonatum, Maianthemum and Smilacina) are in GROUP IV. In other words, our arrangement indicates the distinction of only Clintonia from Polygonateae.

Engler's Convollarieae is divided into two subtribes, viz Convollarieae-Aspidistreae and Convollarieae-Convollarineae. These two groups gained the tribal status (Hutchinson, 1973). The distinction between these two tribes was substantiated, on anatomical bases, by Cheadle & Kosakai (1971). Sen (1975) had also accepted these two tribes, he pointed out to the resemblance between Convollarieae (sensu stricto) and Polygonateae. This affinity was suggested by Therman (1956). In our arrangement Convollarieae-Convollarinea is separated from Convollarieae-Aspidistreae, in GROUP IV and GROUP III respectively. Our results also substantiate Sen's (1975) idea about the close relationship of Polygonateae and Convollarieae. GROUP IV includes Polygonateae (except Clintonia) and Convollaerieae (sensu stricto).

Engler's Asparageae includes Asparagus, Ruscus and Danea. The relationship of these genera raised serious taxonomic debates. Hutchinson (1973) retained this tribe to include only Asparagus, while the other two genera are Ruscaceae. Takhtajan (1969) and Dahlgren (1976) had suggested the family status for Asparagus. However, Sen (1975) stated that there is no cogent cytological evidence for that status. Also El-Gazzar & Badawi (1975) did not warrant enough distinction to erect separate family for Asparagus. In our arrangement these 3 genera are grouped together even to the 25 groups level (Badawi & Elwan, 1986). Such grouping, nevertheless, may be due to their pronounced distinction from other liliaceous taxa rather than their similarity.

The tribe Pariideae in Engler's (1888) system is Medeoleae by Bentham and Hooker; including Medeola, Scoliopus, Paris and Trillium. Takhtajan (1969) and Cronquist (1968) kept also this tribe in Liliaceae. A distinct family, Trilliaceae was erected for these genera (Hutchinson, 1973). However, in our arrangement Pariideae seems to fit in quite well with other Asparagoideae in Group IV. Chatterji & Sharma (1970) had also on cytological bases suspected the recognition of a distinct family for such group of genera.

Table 2. Comparison between our arrangement (Badawi & Elwan, 1986) and that of Engler at the nine Groups level. Numbers between parentheses represent the number of species out of the total examined.

GROUP I (8/255)	
Group A:	
Melanthoideae-Veratreae	(8/8)
GROUP II (69/255)	
Broup B:	
Melanthioideae-Helonieae	(2/4)
Melanthioideae-Colchiceae	(6/6)
Lilioideae-Scilleae	(2/42)

Group D:

Melanthioideae-Tofieldieae	(2/3)
Melanthioideae-Helonieae	(1/4)
Melanthioideae-Anguillarieae	(5/5)
Asphodeloideae-Asphodeleae-Asphodelinae	(2/10)
Asphodeloideae-Johnsoniaea	(2/3)
Allioideae-Agapantheae	(1/4)
Allioideae-Allieae	(26/31)
Allioideae-Gilliesieae	(3/3)
Lilioideae-Tulipeae	(17/17)

GROUP III (117/255)

Group E:

Asphodeloideae-Aloineae-Aloinae	(7/7)
Lilioideae-Scilleae	(2/42)

Group F:

Melanthioideae-Tofieldieae	(1/3)
Melanthioideae-Helonieae	(1/4)
Asphodeloideae-Asphodeleae-Asphodelinae	(8/10)
Asphodeloideae-Asphodeleae-Anthericinae	(14/14)
Asphodeloideae-Asphodeleae-Chlorogalinae	(1/1)
Asphodeloideae-Asphodeleae-Odontostominae	(1/1)
Asphodeloideae-Asphodeleae-Eriosperminae	(3/3)
Asphodeloideae-Asphodeleae-Dianellae	(1/1)
Asphodeloideae-Hemerocallideae	(4/4)
Asphodeloideae-Aphyllantheae	(1/1)
Asphodeloideae-Johnsonieae	(1/3)
Asphodeloideae-Lomandreae	(1/2)
Alloideae-Agapantheae	(3/4)
Allioideae-Allieae	(5/31)
Lilioideae-Scilleae	(38/42)
Dracaenoideae-Yucceae	(2/2)
Dracaenoideae-Nolineae	(3/3)
Dracaenoideae-Dracaeneae	(7/7)
Asparagoideae-Polygonateae	(2/13)
Asparagoideae-Convollarieae-Aspidistrinae	(1/1)
Ophiopogonoideae	(6/6)
Aletroideae	(4/4)

GROUP IV (61/255)

Group G:

Melanthioideae-Uvularieae	(10/12)
Asparagoideae-Polygonateae	(1/13)
Asparagoideae-Pariideae	(4/4)
Luzuriagoideae	(1/4)

Group H:

Melanthioideae-Uvularieae	(2/12)
Herrerioideae-Herrerieae	(3/3)
Asphodeloideae-Dasypogoneae	(1/1)
Asparagoideae-Polygonateae	(5/13)
Luzuriagoideae	(3/4)
Smilacoideae	(8/8)

Group I:

Asphodeloideae-Lomandreae	(1/2)
Asparagoideae-Asparageae	(16/16)
Asparagoideae-Polygonateae	(5/13)
Asparagoideae-Convollarieae-Convollarinae	(1/1)

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